Molecular and morphological analysis of Pacific reed warbler specimens of dubious origin, including *Acrocephalus luscinius astrolabii*

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Summary.—Old museum specimens of Pacific reed warblers with dubious origins were sampled genetically. We studied two specimens described as a subspecies of Nightingale Reed Warbler *Acrocephalus luscinius astrolabii*, the origin of which has been tentatively attributed to Micronesia. However, phylogenetic analysis revealed that these specimens are closely related to Tuamotu Reed Warbler *A. atyphus*. We combined these results with morphological characters and a re-evaluation of label data, on the basis of which we suggest that these birds represent an extinct taxon from the Gambier Islands. Other specimens of dubious origin probably came either from the Society or from the Marquesas Islands.

Reed warblers (genus *Acrocephalus*) are widespread in the Pacific, from Micronesia and Australia east to Hawaii and Eastern Polynesia, although several of these insular populations or taxa have reportedly become extinct since the 19th century. Extinctions have been recorded in at least five archipelagos: Mariana (Guam, Pagan), Kiribati (= Line Islands, Fanning), Hawaii (Laysan), Society (Leeward Islands and Mo'orea) and Tuamotu (several atolls) (Holyoak & Thibault 1984, Pratt *et al.* 1987, Fleischer *et al.* 2007, Cibois *et al.* 2008). In the Gambier Islands (Fig. 1), the presence of reed warblers was documented by

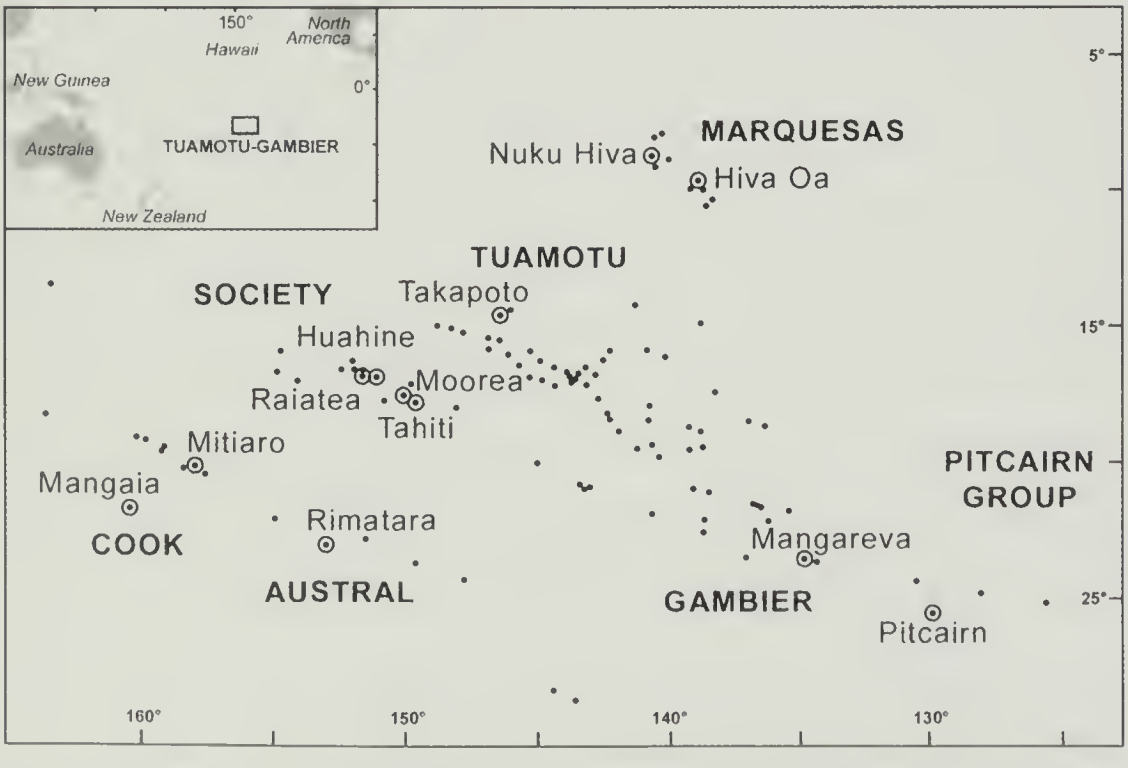

Figure 1. Map of Eastern Polynesia showing islands mentioned both in the text and in Fig. 2. Encircled dots indicate species treated in the phylogenetic tree, except for Nihoa (Hawaii), Kiribati (Line Islands) and Australia, which are not figured.

European navigators during the 19th century (see Discussion) and two specimens held at the Muséum National d'Histoire Naturelle (MNHN, Paris) were suspected to come from there, although their origin was disputed (Holyoak & Thibault 1978). As part of efforts to construct a comprehensive phylogeny of Pacific reed warblers, these specimens were sampled genetically, as were four others of unknown origin from MNHN and the Natural History Museum (BMNH, Tring). Here we present the genetic results for these specimens of dubious origins, compare them to the label information and to their morphological features, and finally discuss their putative identification at species level.

Material and methods

The specimens sampled are described in Table 1. Museum samples were washed with sterile water before extraction, and total genomic DNA was extracted from small pieces (0.5–1.0 cm^2) of skin using a commercial kit (DNeasy Tissue Kit; Qiagen, Valencia, CA, USA). Standard extraction protocols were followed except that the time of proteinase digestion was increased from two to 12 hours, with an additional volume (20 µl) of proteinase K. All tubes and reagents were UV-treated for 30 minutes before use and extraction tubes containing no sample were used as a control for contamination. DNA extracted from museum specimens was degraded, so fragment sizes for amplification were small (*c.*200 bp). Specific primers designed for Pacific reed warblers are given in Cibois *et al.* (2007): sections of both genes were amplified using overlapping fragments. PCR amplifications were performed in 25µl reactions with 2 µl of template and 0.4 µM final concentration for primers. The thermocycling procedure started with an initial denaturation of three minutes at 95°C, followed by 40 cycles of 30 seconds at 95°C, 40 seconds at annealing temperature (50°C), and 40 seconds at 72°C for elongation. PCR products were purified using a Qiagen purification kit and sequenced directly (ABI Prism 377 automated DNA Sequencer) using the same primers. Contiguous sequences derived from the set of sequence fragments were created using Sequencher (Genecodes, Ann Arbor, MI, USA). Sequences were aligned to Pacific and continental reed warbler sequences available in GenBank (Leisler *et al.* 1997, Helbig & Seibold 1999, Cibois *et al.* 2007, Fleischer *et al.* 2007, Cibois *et al.* 2008). The data were subjected to Bayesian inference using MrBayes 3.1.2 (Ronquist & Huelsenbeck 2003), with models selected using MrModeltest 2.3 and the AIC criterion (Nylander 2004). We ran two independent runs of four Markov chains for one million generations each. Markov chains were sampled every 100 generations, with a 10% burn-in period.

In the light of the genetic results, we compared the six individuals of dubious origin to reed warblers specimens held in the American Museum of Natural History (AMNH, New York) and the Übersee-Museum Bremen (UMB) collections for the following measurements: wing length (the distance between the carpal joint and tip of the flattened wing), bill length from tip to skull, bill length from tip to rear of nostril, bill width (at rear of nostril), tarsus length (from notch of inter-tarsal joint to lower edge of last complete scale), hindclaw length (chord from tip of claw to edge of the skin of nail), and tail length (from insertion of central pair of feathers to tip of longest rectrix). All measurements were made by AC.

Results and Discussion

Partial cytochrome-*b* gene sequences of 879 bp were obtained for MNHN 1982-769 and MNHN 1847-23. Shorter sequences were obtained for MNHN 1982-768 (412 bp), BMNH 1855.12.19.85 and BMNH 1846.7.29.6 (419 bp). Amplifications were unsuccessful for BMNH 1846.7.29.5. New sequences were deposited in GenBank under accession numbers HQ851084–851087. The alignment was straightforward with no indel, as expected for

TABLE 1

Data on the specimens studied (in bold). MNHN = Muséum National d'Histoire Naturelle, Paris. BMNH = Natural History Museum, Tring. Additional measurements (mean ± standard deviation) are given for four other taxa based on specimens examined in the American Museum of Natural History (AMNH) and the Übersee-Museum Bremen (UMB) collections. All measurements are in mm.

Specimen number	Label data	Wing length	Bill length from tip to skull	Bill length from tip to rear of the nostril	Bill width	Tarsus length	Hindclaw length	Tail length	Putative origin
MNHN 1982-768	Philedon chanteur, Astrolabe[1] Mangareva (*Acrocephalus luscinius astrolabii*)	95	37.2	23.2	5.5	32.5	10.0	95	Gambier
MNHN 1982-769	Philedon, Astrolabe[1] Nouheva (*Acrocephalus luscinius astrolabii*)	99	36.9	22.1	5.4	33.2	10.1	94	Gambier
MNHN 1847.23	(*Acrocephalus caffer*) Tongatabu	91	29	16.9	4.4	27.5	7.8	82	Society Islands
BMNH 1846.7.29.5	Tatare otaitensis, Society Islands, coll. Turner	95†	31.7	18.3	5.2	28.7	9.8	92†	Marquesas or Tahiti
BMNH 1846.7.29.6	Tatare otaitensis, Society Islands, coll. Turner	101	36.9	21.4	5.7	31.8	10.6	88	Leeward Islands (Society Islands)
BMNH 1855.12.19.85	Tatare otaitensis, Society Islands, coll. Zool. Soc.	100	30.6	17.1	5.0	31.2	-	90	North Marquesas
AMNH (*n*=16)	*Acrocephalus caffer* Tahiti (Society Islands)	96.8 ± 2.5	34.3 ± 0.9	19.9 ± 0.8	5.2 ± 0.2	32 ± 1	9.0 ± 0.3	91.2 ± 5.0	
AMNH (*n*=15)	*Acrocephalus percernis* Nuku Hiva (North Marquesas)	98.4 ± 3	29.2 ± 1.1	17.6 ± 0.4	5.1 ± 0.2	32 ± 1	9.7 ± 0.4	95.5 ± 8.0	
AMNH 594897	*Acrocephalus musae garretti* Huahine (Leeward Islands, Society Islands)	103	36.8	21.7	5.3	33.2	10.5	103†	
UMB 7947	*Acrocephalus m. musae* Raiatea (Leeward Islands, Society Islands)	101	37.5	21.7	5.4	32.0	10.0	92	
AMNH 190398	*Acrocephalus longirostris* Mo'orea (Society Islands)	104	37.8	22.4	5.3	30.8	9.9	98	
AMNH (*n*=15)	*Acrocephalus atyphus* Fa'aite (Tuamotu)	89.5 ± 2.4	26.5 ± 1.3	15 ± 0.6	4.7 ± 0.4	30.1 ± 0.6	8.3 ± 0.3	90 ± 4	

[1] *Astrolabe* was one of the ships used by Dumont d'Urville's expedition in the Pacific Ocean (1838–39)
† Incomplete length due to feather wear

a protein-coding gene. We translated the nucleotide sequences to proteins using Mega (Tamura *et al.* 2007) and found no stop codon. We detected no contamination in the negative controls. The sequences of MNHN 1982-768 and 1982-769 were identical. The sequence of BMNH 1855.12.19.85 was identical to that of Northern Marquesan Reed Warbler *A. percernis*. The sequence of BMNH 1846.7.29.6 differed by one transversion from the sequence of the Leeward Islands Reed Warbler *A. musae garretti* from Huahine. The sequence of MNHN 1847-23 differed by seven bases (five transitions and two transversions) from Tahiti Reed Warbler *A. caffer*. Uncorrected pair-wise distances are given in Table 2.

Results from the AIC criterion in MrModeltest supported the GTR + I + G model (General Time Reversible + Proportion Invariant + Gamma: Lanave *et al.* 1984, Rodriguez *et al.* 1990) for the dataset. The phylogenetic tree obtained using MrBayes is presented in Fig. 2. Results for the main Polynesian lineages were detailed in previous works so we only focused on the placement of specimens of dubious origin. The two *astrolabii* (MNHN 1982-768 and 1982-769) formed a well-supported clade with *A. percernis* and Tuamotu Reed Warbler *A. atyphus* (0.99 Bayesian posterior probabilities PB). Within this group, *atyphus* and *astrolabii* were sister taxa but with low support (0.74 PB). MNHN 1847-23 was sister taxon to *caffer* with good support (1 PB). BMNH 1855.12.19.85 branched off with *percernis* (same haplotype, 0.97 PB due to the shorter sequence), whereas BMNH 1846.7.29.6 was sister to *musae* (Huahine and Raiatea, Society Islands) with good support (1.0 PB).

MNHN 1982-768 and 1982-769: Acrocephalus luscinius astrolabii.—The labels of these two specimens bear similar handwriting, indicating 'Mangareva, Astrolabe, Philedon chanteur', numbered 151 and registered as number E 8681 in the *Catalogue des Oiseaux* no. 3 of the MNHN ornithological collection for MNHN 1982-768, and 'Philedon, Nouheva [or Nouhiva], Astrolabe' numbered 266, with no registration number, for MNHN 1982-769. In accordance with the label of the first specimen, Lacan & Mougin (1974) suggested that both originated from the island of Mangareva in the Gambier archipelago. However, Holyoak & Thibault (1978) rejected this hypothesis based on the lack of agreement between the labels (Nouheva / Nouhiva, an unknown locality that could be an approximation of Nuku Hiva in the Marquesas) and the similarity in coloration and biometry of the specimens to Nightingale Reed Warbler *A. luscinius* of Micronesia. They proposed a new subspecies, *A. luscinius astrolabii* (type specimen MNHN 1982-768), from an unknown island of Micronesia, tentatively attributed to Yap. Holyoak & Thibault (1978) were influenced by (a) their coloration being very similar to forms of *A. luscinius*, and (b) that the type was registered in the MNHN catalogue as E 8681 following 'D 8681 *Acrocephalus* syrinx K et F. Carolines-Hombron et Jacquinot 1841-106' from Micronesia.

Molecular data suggest that the two *A. l. astrolabii* specimens have the same origin: both possess a unique cytochrome-*b* haplotype and they are more closely related to Northern Marquesan and Tuamotu Reed Warblers than to any other Pacific reed warblers studied, particularly to *A. luscinius* (Fig. 2). The Tuamotu archipelago is the closest group of islands to the Gambier archipelago (Fig. 1). Morphologically the two specimens are distinct from *A. percernis* and *A. atyphus* (Fig. 3), with on average a bill longer than *percernis* and *atyphus*, a wing longer than *atyphus* but similar to *percernis* (Table 2), and brown plumage which recalls more that of *atyphus* than the yellow coloration of Marquesas reed warblers (Pratt *et al.* 1987). Because the labels of both *A. l. astrolabii* specimens mention 'Astrolabe' and both possess a unique haplotype closely related to Tuamotu Reed Warbler, it is probable that they were collected in the Gambier Islands during the Antarctic Expedition commanded by Captain J. S. C. Dumont d'Urville aboard the two ships *Astrolabe* and *Zélée*, with the naturalists J.-B. Hombron and H. Jacquinot. This expedition travelled extensively in the

TABLE 2

Pair-wise sequence divergence found in the cytochrome-*b* sequences (% uncorrected values). The five specimens studied are indicated in bold.

	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19
1. *A. aequinoctialis* EF156278																			
2. MNHN 1982.768	3.3																		
3. MNHN 1982.769	3.3	0.0																	
4. *A. atyphus* EF156281	3.0	0.9	0.9																
5. *A. australis* AJ004305	1.5	3.0	3.0	3.3															
6. *A. caffer* EF156308	2.7	1.2	1.2	1.5	2.4														
7. *A. familiaris kingi* EU119965	3.3	3.6	3.6	3.9	3.0	3.0													
8. *A. musae garretti* EU303306	2.7	2.1	2.1	2.4	3.0	2.1	3.0												
9. *A. m. musae* EU303310	3.6	3.0	3.0	3.3	3.9	3.0	3.9	0.9											
10. *A. kerearako kaoko* EF156291	2.7	3.6	3.6	3.9	3.0	3.0	3.6	3.6	4.5										
11. *A. k. kerearako* EF156292	2.4	2.7	2.7	2.4	2.7	2.1	3.3	2.4	3.0	2.1									
12. *A. longirostris* EU303308	3.3	1.5	1.5	1.8	3.6	2.1	3.6	1.8	2.4	4.2	2.7								
13. *A. mendanae* EF156287	0.3	3.0	3.0	2.7	1.2	2.4	3.0	2.4	3.3	2.4	2.1	3.0							
14. MNHN 1847.23	3.3	1.8	1.8	2.1	3.0	0.6	3.6	2.1	3.0	3.6	2.7	2.7	3.0						
15. BMNH 1846.7.29.6	2.7	1.8	1.8	2.1	3.0	1.8	3.0	0.3	1.2	3.6	2.1	2.1	2.4	1.8					
16. BMNH 1855.12.19.85	3.3	0.6	0.6	1.5	3.0	1.2	3.6	2.1	3.0	3.6	2.7	1.5	3.0	1.8	1.8				
17. *A. percernis* EF156299	3.3	0.6	0.6	1.5	3.0	1.2	3.6	2.1	3.0	3.6	2.7	1.5	3.0	1.8	1.8	0.0			
18. *A. rimitarae* EF156305	2.4	2.1	2.1	2.4	2.1	1.5	3.3	2.4	3.3	2.1	1.2	3.0	2.1	2.1	2.1	2.1	2.1		
19. *A. taiti* AJ004308	4.8	4.5	4.5	5.4	4.5	3.9	5.7	4.8	5.7	5.7	4.8	5.4	4.5	4.5	4.5	4.5	4.5	4.2	
20. *A. luscinius* HQ844366	0.6	3.3	3.3	2.4	1.5	2.1	3.3	2.7	3.6	2.7	2.4	3.3	0.3	2.7	2.7	3.3	3.3	2.4	4.8

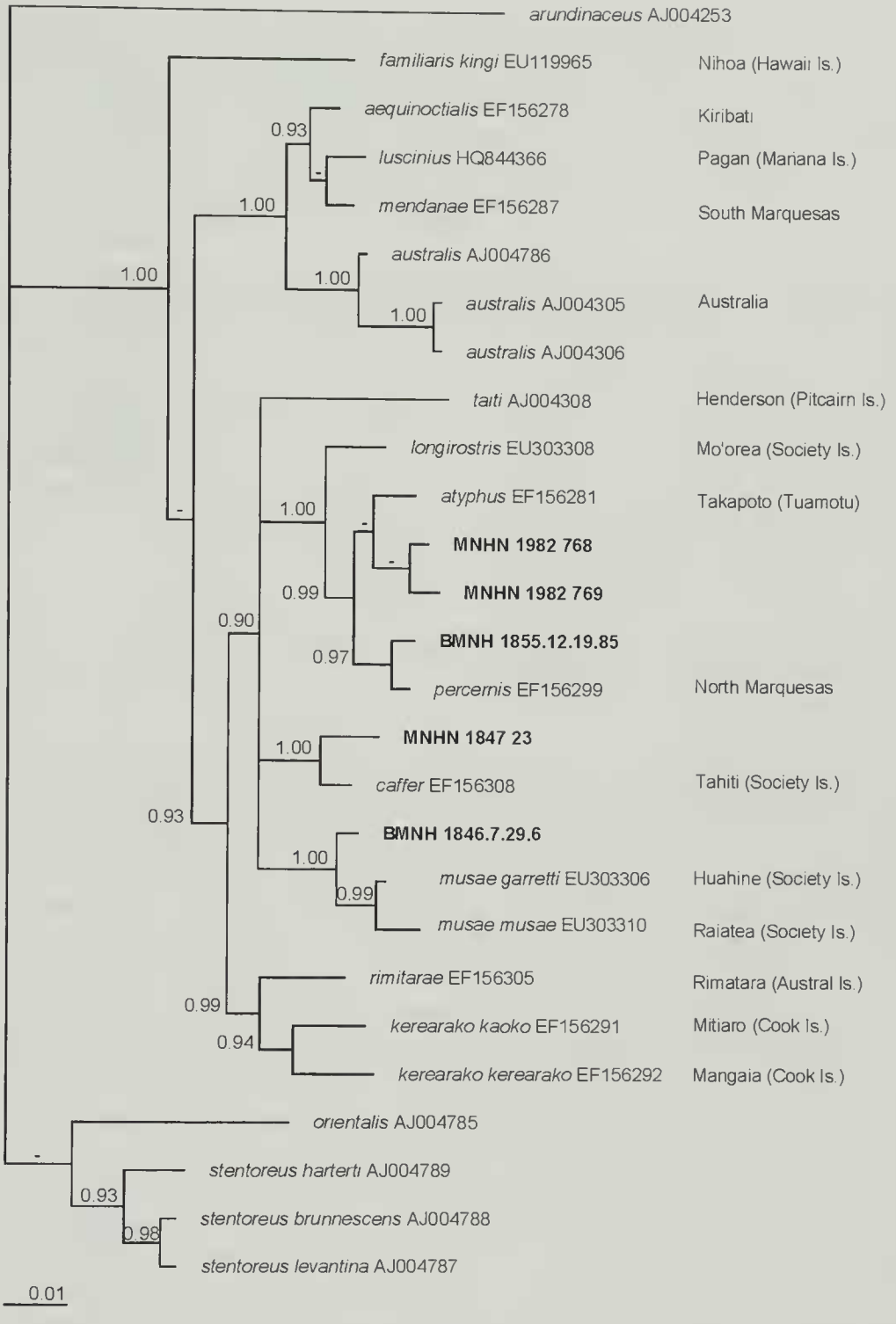

Figure 2. Phylogenetic tree estimated using Bayesian inference and partial cytochrome-*b* sequences. Numbers by nodes refer to posterior probabilities; dashes indicate probabilities inferior to 0.90. GenBank numbers are indicated beside the taxon name, and the specimens of dubious origin are indicated in bold.

tropical Pacific in 1838–39 and visited numerous islands in Polynesia and Melanesia, as well as a few in Micronesia. They reached Mangareva on 3 August 1838 (Dumont d'Urville 1842) and visited the four main islands, Mangareva, Aukena, Taravai and Akamaru. A detailed catalogue of the ornithological collection was never published as explained in Jacquinot & Pucheran (1853) but according to the labels of specimens still present at MNHN, the expedition collected at least these two reed warblers, a Pacific Reef Heron *Egretta sacra* (MNHN 195) and the type specimen of Tuamotu Kingfisher *Halcyon gambieri* (MNHN 2006-555).

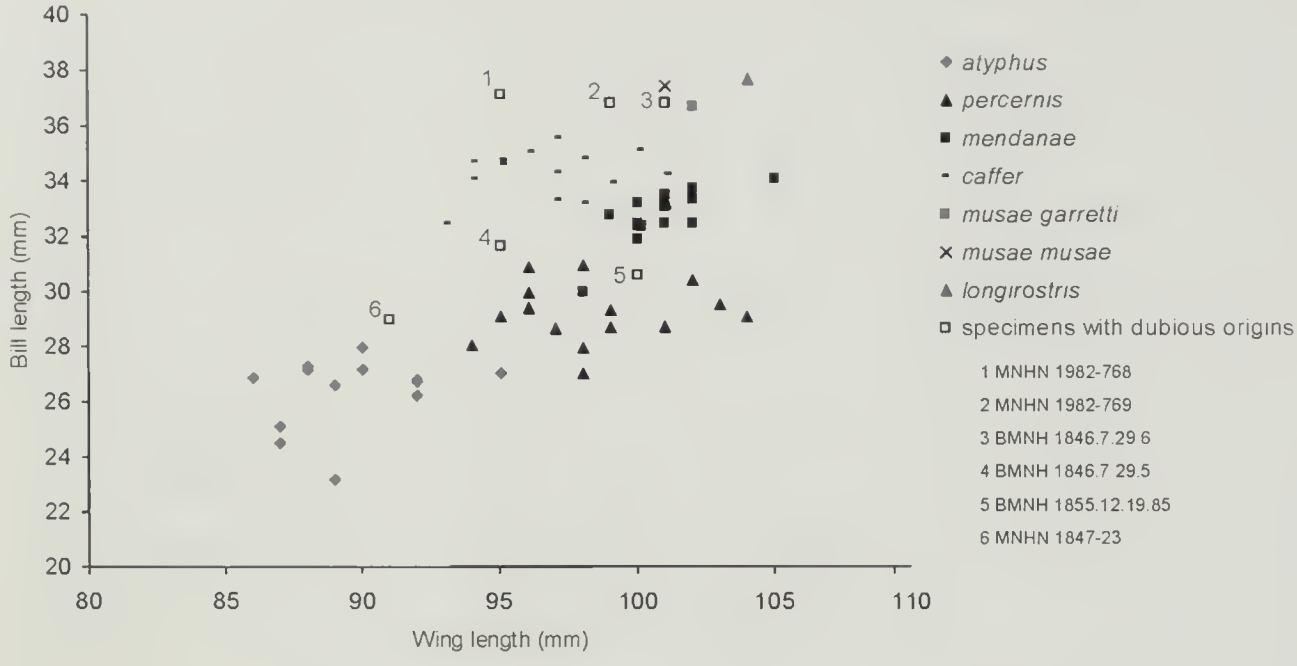

Figure 3. Bill length (from tip to skull) vs. wing length for those specimens of dubious origin and several eastern Polynesian reed warbler taxa (see Table 1).

To our knowledge no other reed warbler specimen from the Gambier Islands exists in ornithological collections. In addition to Dumont d'Urville's expedition, two other expeditions reached the archipelago during the first half of the 19th century and recorded reed warblers. During his expedition to the Bering Strait and the Pacific islands, Frederick William Beechey visited the Gambier Islands for a few days in January 1826. There he observed a bird that corresponds quite well to a reed warbler: 'a species of turdus, somewhat resembling a thrush in plumage, but smaller, possessing a similar though less harmonious note' (Beechey 1832: 123). Two years after Dumont d'Urville's expedition, Pierre-Adolphe Lesson, who served as a surgeon on the *Pylade*, visited Mangareva for nine days in April 1840, where he observed and collected a reed warbler ('Je tuais aussi un oiseau du genre philedon': Lesson 1844: 62). Unfortunately the fate of this specimen, like most of the ornithological collection gathered by the two Lesson brothers, is unknown. Additional evidence suggests that reed warblers were still present on the Gambier Islands during the second part of the 19th century. In their comments on specimens collected by Andrew Garrett in the 1870s for the Godeffroy Museum in Hamburg, Schmeltz & Krause (1881: 238) mentioned that reed warblers were likely found in the Gambiers ('Soll auch auf den Gambier-Inseln vorkommen'), although no specimen was specifically mentioned. Wiglesworth (1891) also included the Gambier Islands in the distribution of *Acrocephalus* (with Garrett as collector), but we do not know whether he had access to a specimen or if he merely based this information on Schmeltz & Krause's comment. In the early 20th century, the birds were never observed again by ornithologists (e.g. the Whitney South Sea Expedition in 1922) or naturalists (e.g. Alvin Seale in April 1902; Seale 1901–02) but two testimonies provide the last evidence of the former presence of reed warblers in the Gambiers. In 1922, the chief of Taravai, one of the islands of the archipelago, described a bird similar to a reed warbler but which had not been seen for 30 or 50 years to Ernst Quayle, the collector of the Whitney South Sea Expedition organised by the American Museum of Natural History (Quayle ms; vol. K, p. 122). During the Mangarevan Expedition organised by the Bernice P. Bishop Museum in 1934, the archaeologist Kenneth Emory noted that the Polynesians of the

Gambiers still used the name 'Komako' for a bird no longer present there (Te Rangi Hiroa 1938): it is the current name for *Acrocephalus* spp. in the Marquesas and some Tuamotu islands (Holyoak & Thibault 1984), and also that mentioned by Lesson (1844) and Tregear (1899). No fossil remains of reed warblers have been obtained from archaeological sites in the Gambiers (Worthy & Tennyson 2004), but bones of small passerines have rarely been found by such surveys on Pacific Islands (Steadman 2006).

Other specimens of dubious origin.—Peale (1848) included Samoa and Tonga (= Tongatabu) as localities for specimens of *Acrocephalus* reed warblers collected during the United States Exploring Expedition in the Pacific Ocean (1838–42). However, Finsch (1872) did not obtain such birds in Samoa and Tonga and doubted that a reed warbler inhabited these islands. Specimen MNHN 1847-23 is labelled 'Tongatabu', but genetically this individual is closely related to Tahiti Reed Warbler. It is obviously smaller than other individuals from Tahiti (Table 1, Fig. 3) but its plumage is typical of pale phase Tahitian birds, being yellow below and olive above with pale feather fringes (Pratt *et al.* 1987). Thus plumage and genetic data suggest that this specimen was probably collected in the Society Islands, maybe Tahiti, but not on Tonga, in accordance with the absence of confirmed information on the past presence of reed warblers in Central Polynesia (Tonga or Samoa). We propose to classify this bird as *A. caffer* (Society Islands).

The three specimens held at BMNH were provisionally all classified as '*Acrocephalus caffer*?', and were all probably collected during the second quarter of the 19th century. They possess bright yellow underparts that correspond to either the Society Islands or the Marquesan birds. BMNH 1855.12.19.85 possesses the same cytochrome-*b* haplotype as Northern Marquesan Reed Warbler: its bill is shorter than birds from the Society Islands and corresponds well to that of *A. percernis* (Fig. 3). We propose to classify this specimen under *A percernis* subsp. (Marquesas Islands), with uncertainty regarding the island and subspecies concerned. The two other specimens were collected by Turner, a dealer who supplied 13 specimens of Pacific island birds in 1846, registered under 1846.7.29.1–13. Neither warbler specimen has an original label, only the museum ones which state 'Society Is.' (Table 1), but the register indicates 'Noukaiva' for these two specimens (R. Prŷs-Jones *in litt.* 2010). The DNA sequence obtained for BMNH 1846.7.29.6 contradicts the register information, as this individual is sister taxon to the Leeward Islands reed warblers (Huahine and Raiatea, Society Islands) with good support in the phylogenetic tree (Fig. 2). Moreover, its measurements are similar to those of the taxon from Huahine *A. musae garretti* (Table 1, Fig. 3). Reed warblers are known only from Huahine and Raiatea (two populations extinct today; Cibois *et al.* 2008) but the former distribution of reed warblers in the Leeward Islands could have included other localities. We propose to classify this bird as *A. musae* subsp. (Leeward Islands), with uncertainty regarding the island and subspecies. Unfortunately no sequence was obtained for BMNH 1846.7.29.5. The bill of this specimen is smaller than that of warblers from Tahiti and could correspond to Marquesan birds (Fig. 3), in accordance with the register information, but uncertainty regarding the provenance of this specimen persists.

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